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Author's post-print version

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Associated publication: This manuscript has been published in the *British Journal of Developmental Psychology* and the published article can be found with following DOI: https://doi.org/10.1111/bjdp.12101

Monitoring others' errors:

The role of the motor system in early childhood and adulthood

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Word count (exc. figures/tables): 4989

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The authors declare no competing financial interests.

Acknowledgments

We would like to thank all children and parents for participating in this study. Moreover, we thank our laboratory managers Angela Khadar and Margret van Beuningen as well as our colleague Birgit Knudsen for their help. We also acknowledge the technical support from the Technical Support Group at Radboud University Nijmegen.

Abstract

Previous research demonstrates that from early in life our cortical sensori-motor areas are activated both when performing and when observing actions (mirroring). Recent findings suggest that the adult motor system is also involved in detecting others' rule violations. Yet, how this translates to everyday action errors (e.g. accidentally dropping something) and how error-sensitive motor activity for others' actions emerges is still unknown. In this study, we examined the role of the motor system in error monitoring. Participants observed successful and unsuccessful pincer grasp actions while their EEG was registered. We tested infants (8- and 14-month-olds) at different stages of learning the pincer grasp and adults as advanced graspers. Power in Alpha- and Beta-frequencies was analyzed to assess motor and visual processing. Adults showed enhanced motor activity when observing erroneous actions. However, neither 8- nor 14-month-olds displayed this error-sensitivity, despite showing motor activity for both actions. All groups did show similar visual activity, i.e. more alpha-suppression, when observing correct actions. Thus, while correct and erroneous actions were processed as visually distinct in all age groups, only the adults' motor system was sensitive to action correctness. Functionality of different brain oscillations in the development of error monitoring and mirroring are discussed.

Introduction

An important aspect of understanding others' actions is the detection of errors in others' behavior. Monitoring others' mistakes is at the core of social learning and constitutes the basis for flexible adaptation of actions (Botvinick et al., 2001), a skill which is relevant for establishing successful social interactions (Bekkering et al., 2009; Vesper et al., 2010). Common action errors, occurring daily, are an essential source for learning new actions, improving existing action skills and avoiding action mistakes, skills which are especially important in early childhood. Despite its relevance, little is known about how the infant brain monitors the correctness of others' actions. A potential mechanism that might facilitate monitoring others' behavior is the mirror mechanism (Rizzolatti & Fogassi, 2014), which refers to the overlap in neural activation during action execution and observation (henceforth called mirroring). From early in life cortical sensori-motor areas are active both when performing own and observing others' actions (Saby, Marshall & Meltzoff, 2012; Southgate et al., 2010, van Elk et al., 2008). This finding is interpreted by some as a basis for understanding others' actions and intentions (Bekkering et al., 2009; Hari & Kujala, 2009). In addition, recent findings suggest that the adult motor system (including premotor and primary sensori-motor areas) is also involved in error monitoring (Koelewijn et al., 2008). This evidence is, however, limited to observing the violation of arbitrary task-rules. To what extent everyday action errors, such as accidentally dropping a glass, also elicits this error-related mirroring remains unclear both in infants and adults. Therefore, the aim of this study was to investigate the role of the motor system in monitoring common action errors across development.

Two streams of research need to be considered, one focusing on error monitoring (see Holroyd & Coles, 2002) and another one focusing on mirroring (e.g. Blakemore & Decety, 2001). Evidence from electroencephalography (EEG) and functional magnetic resonance imaging (fMRI) studies on adult error processing suggests a key role of the medial frontal cortex in monitoring own errors (Carter et al., 1998; Gehring et al., 1993; Ullsperger & von Cramon, 2001). Speeded response

paradigms have often been used to investigate neural activity in adults during the performance of errors (e.g. Falkenstein et al., 2000). Additional studies have shown neural processing of own errors similar to adults in 4-year-olds (Rueda et al., 2004) and 10-year-olds (Santesso, Segalowitz & Schmidt, 2006).

The second line of research has demonstrated close links between the processing of observed actions and the execution of actions (Hari & Kujala 2009; Rizzolatti & Craighero 2004). In both infants and adults, electrophysiological data indicate motor-related brain activation during both action observation and execution (Hari, 2006; Lepage & Théoret 2006; Marshall, Young & Meltzoff, 2011; Muthukumaraswamy & Johnson, 2004). Moreover, the violation of expected movements elicited enhanced motor activation during observation in infants (Stapel et al., 2010). In their study, however, the observed actions were unexpected but intentional which is in contrast to typical errors which are also unexpected but accidental.

More recently, studies have integrated both lines of research. In particular, studies with adults have investigated how the correctness of observed actions modulates action processing (de Bruijn, Schubotz & Ullsperger, 2007; Koelewijn et al., 2008). Converging findings demonstrated that monitoring others' actions is based on the same neural underpinnings as monitoring one's own actions (Malfait et al., 2010; van Schie et al., 2004). Recently, the involvement of the sensori-motor cortex in monitoring others' actions was demonstrated using MEG: Koelewijn and colleagues (2008) showed that violating an arbitrary task-rule, by responding with an incorrect button press to a certain color-cue, leads to enhanced motor activity. More specifically, they found stronger suppression and rebound of central Beta-power (i.e. indicating enhanced motor activity) during the observation of erroneous compared to correct actions. Thus, in adults, the correctness of observed actions modulates processing in the observer's motor system when errors represent task-rule violations. Moreover, the oscillatory pattern during error observation resembled the pattern of performing an erroneous action in the same participants. Hence, the findings suggest that the motor activation provides an important basis for monitoring others' action success.

To date, little is known about how error monitoring in the motor system develops in infants. Potentially, motor development, and hence motor experience underlies the ability to dissociate correct from erroneous actions. Support for this notion comes from Aglioti and colleagues (2008), who found that expert players showed enhanced motor excitability when watching erroneous compared to correct basket shots. No difference in motor excitability was found in novices. Other neurocognitive studies have shown that action experience influences mirroring in infants and adults (Cannon et al., 2015; van Elk et al., 2008, Calvo-Merino et al., 2005), and recent findings suggest that effects of action experience on mirroring are stronger than observational experience alone (Gerson et al., 2015). Additionally, many behavioral infant studies stress the influence of action experience on the perception of others' actions (for a review see Hunnius & Bekkering, 2014; Woodward, 2009). Since the motor repertoire influences the processing of others' actions (van Elk et al., 2008), motor experience might also be important to discern erroneous from successful actions (e.g. Aglioti et al., 2008).

To investigate the role of the motor system in processing others' errors, we conducted an EEG study. We tested three groups (8-month-olds, 14-month-olds, adults) with different levels of expertise in performing pincer grasps (i.e. grasping small objects using the tip of index finger and thumb). Unlike 14-month-olds and adults, 8-month-olds cannot yet grasp small objects with a pincer grasp. Based on previous research (Koelewijn et al., 2008), we hypothesized that the observation of erroneous compared to correct actions would result in enhanced motor activation. Moreover we expected an error-sensitivity in adults and infants who can perform the pincer grasp, but not infants with limited motor expertise.

The study consisted of an action observation and execution phase. First, participants observed correct and erroneous pincer grasp actions. Subsequently, their ability to perform pincer grasps was assessed. Motor-related brain activity during action observation and execution was analyzed as indexed by power differences in the Mu- and Beta-frequency ranges (Lepage & Théoret 2006; Muthukumaraswamy & Johnson, 2004; Saby, Marshall & Meltzoff, 2012). Furthermore, to

address the specificity of error-related responses in the motor system we assessed activity of the visual system. Visual processing during action observation was analyzed as indexed by power differences in the Alpha-frequency range over occipital sites.

Method

Participants

Twelve 8-month-olds, ten 14-month-olds and ten adults were included in the final sample (Table 1). Infants were selected from a database of families volunteering to participate in child studies. An additional 25 8-month-olds and 25 14-month-olds were tested but excluded due to unwillingness to wear the EEG cap (*N*=2, 14-month-olds), technical problems (*N*=3, 8-month-olds) or insufficient artifact-free trials given a minimum amount of nine trials per condition (*N*=22, 8-month-olds; *N*=23, 14-month-olds). The high attrition rate follows the strict criteria for our EEG analysis, including only trials were infants were attending and not moving and is typical for comparable EEG experiments (cf. Southgate et al., 2010; Stapel et al., 2010; Stets, Stahl & Reid, 2012). This study was approved by the local ethical committee.

Stimuli & Materials

Video stimuli

Thirty-two videos displaying a manual action on a small object were created (Figure 1a). With each object, a successful and an erroneous grasping action were recorded. Each video had a duration of approximately 6s and started with a hand entering the scene from one side (50% from the right). After about 1.3s, the initially ambiguous reaching movement unfolded into the unambiguous phase on which all analyses were based: In the error condition, the actor repeatedly tried but failed to pick up the object; in the correct condition, the actor picked up the object and moved it around, following a similar movement path as in the error condition. On average, eight such movements were performed per stimulus video in both conditions. Both conditions included object-directed, transitive actions. To ensure that the videos displayed authentic grasping errors, actors were blind-folded during recordings of erroneous actions. Identical to Schippers and colleagues (2010), we determined motion energy for each video, by calculating the sum of the squared differences in the red, green,

and blue color-channels between two consecutive frames for every pixel and then summing over all pixels and frames. A paired sample t-test verified no significant differences in the amount of motion energy between the correct and erroneous videos ($t(7)= -1.67$ $p=0.14$), controlling for low-level differences in the stimulus features.

Proficiency assessment

To test infants' motor proficiency, we designed a device to assess pincer grasp performance (Figure 1b), which consisted of a wooden frame installed on a box on which differently sized beads could be fitted. Each bead was surrounded by two colored circles and was fixed with a string in the back of the board.

Procedure

The session consisted of an action observation phase followed by an action execution phase. EEG was recorded throughout and the infants sat on their parent's lap in a shielded testing room. During the action observation phase, infants were presented with video stimuli displayed on a screen (50cm distance). Each video was preceded by a 1s fixation cross serving as a baseline. Videos of correct and erroneous actions were presented in pseudo-random order with an equal amount of videos presented for each condition. Each video was shown maximally twice resulting in a maximum of 64 trials. Background music was played unrelated to stimulus presentation. After all trials were completed or when infants became fussy, the action execution phase was initiated. The experimenter placed the pincer grasp device in front of the infant and demonstrated how to grasp and pull out the bead once. After bringing the bead back to the original position, the infants were given 1 minute to pull out the bead. First, infants were presented with a large bead (diameter=5mm), then with a smaller one (diameter=3mm) to slightly increase task difficulty. The testing session was video-recorded for offline movement coding and behavioral analysis.

The procedure was identical for adults, except for the action execution phase during which a cue signaled them to perform the grasping action. For each of the two beads, adults were asked to grasp and pull out the bead five times resulting in ten grasping actions.

EEG recordings

EEG data was collected using 32 Ag/AgCl active electrodes which were placed in either infant- or adult-sized actiCaps (Brain Products, Munich) arranged in the 10-20 system. All electrodes were online referenced to FCz and offline re-referenced to the average of all electrodes, after excluding extremely noisy channels. On average, 0.75 channels (range:0-3, *SD*=1.14) were excluded for the 8-month-olds and 2.8 channels (range:0-17, *SD*=5.16) for the 14-month-olds, respectively. The signal was amplified using BrainAmp amplifiers, band-pass filtered (.1-125Hz) and digitized at 500Hz. Impedances were kept below 60kΩ for infants and 25kΩ for adults.

EEG data analysis

EEG data was analyzed using Fieldtrip, an open source Matlab toolbox (Oostenveld et al., 2011). In line with suggestions by Marshall and Meltzoff (2011), we considered action execution, observation and topography for our analysis (i.e. assessing motor and visual processing). First, we used the contrast between action execution and baseline over central sites to identify sample-specific frequency bands involved in motor processing. Frequency ranges in which significant suppression during action execution was found were then used for the analysis of conditional differences in mirroring. In addition, we analyzed differences in posterior Alpha to assess visual processing.

Action execution

In order to determine EEG segments in which infants performed a pincer grasp, video recordings were coded offline. For the 14-month-olds, EEG-epochs were extracted during which they successfully performed pincer grasps and pulled out the bead. For the 8-month-olds, epochs were

selected during which they reached out, touched and manipulated the beads, mostly without successfully grasping them. The epochs were then cut into 1s segments. Analogously, for the adults we used the first second after each movement cue which contained reaching and grasping movements. For the EEG analysis of the action execution phase, two 8-month-olds and one 14-month-old had to be excluded due to absence of any artifact free trials.

For the action execution and observation data (see below), each 1s segment was demeaned to the entire segment and a DFT filter was applied to remove line noise. By careful visual inspection, any remaining segments containing artifacts were rejected. Subsequently, we performed frequency analysis using the multitaper method (Hanning taper, 2Hz spectral smoothing).

Determining Mu- and Beta-frequency ranges

To determine the frequency ranges, we inspected the grand average power spectrum in the 2 to 30Hz range for the baseline and action execution condition averaged across central electrode sites (C3,C1,Cz,C2,C4). For Mu- and Beta-ranges separately, we then visually determined the windows in which the power during action execution was lower compared to baseline (Figure 2), resulting in age-specific frequency band widths.

We only continued with the analysis of the action observation phase for a particular frequency and age group if significant suppression during execution (i.e. index of motor activity) was confirmed for that group and frequency band.

Motor processing

The focus of the current study was to investigate differences in mirroring between the error and correct conditions. Critical to the analysis of action processing during observation is the exclusion of any epochs of participant movement . Hence, we coded the infants' behavior frame by frame as to include only EEG segments during which infants were watching the screen and sitting still. Selected

periods were divided into 1s segments and separately processed for the two condition. Artifact rejection and frequency analysis were performed as for the action execution segments.

For statistical comparison of the two conditions, we normalized the band specific power over sensori-motor cortices (C3,C1,Cz,C2,C4) per condition by dividing it by the baseline power and taking the log of that ratio. To test for differences in action processing during observation we used these normalized power values to conduct a mixed ANOVA per frequency range with within-subject factor Condition and between-subject factor Age Group. In addition, one sample t-tests per group were used to test whether participants showed suppression of power (i.e. motor activation) during action observation.

Visual processing

To assess differences in visual processing, we analyzed posterior Alpha, by investigating the same frequency range as for the Mu-band but averaged over posterior sites (O1,Oz,O2). Data processing, analysis and statistics were identical to the Mu-band analysis.

Time-resolved and topographic analysis for adults

Data quality of the adult age group allowed to additionally examine the time-course and topography of the action processing during observation. A time-resolved spectral power analysis was conducted using Fourier transform (500ms sliding Hanning taper, spectral smoothing of 3Hz) calculating power estimates between 1Hz and 40Hz. The resulting time-frequency representations (TFRs) were obtained for central and occipital sites separately and represent the direct contrast between conditions ([error-correct]/[error+correct]). To investigate the topographic distribution of the Alpha- and Beta-effects, the normalized differences for the respective frequency ranges were collapsed for each electrode over the unambiguous phase of the stimulus videos.

Results

Behavioural performance

The 8-month-olds never pulled out the beads using the pincer grasp. On the contrary, all but one 14-month-old pulled out the beads successfully (*M*=7.4 times, range:0- 20). More specifically, they succeeded on average 4.2 times (range:0- 8) for the large bead and 3.2 times (range:0=14) for the small bead. The 14-month-olds also hardly ever manipulated the bead with the whole hand but used their index finger, thumb or both.

EEG results

Determining Mu- and Beta-frequency ranges

We determined the following Mu- and Beta-frequency ranges: 8-month-olds (Mu:6-9Hz, Beta:12-15Hz), 14-month-olds (Mu:6-10Hz, Beta:14-18Hz), adults (Mu:7-12Hz, Beta:16-25Hz).

Action execution vs. baseline

Results of the one-tailed one-sample t-tests (Table 2A) showed significant suppression of Mu- and Beta-power during action execution for 14-month-olds (Mu: *M*=-.556, *SD*=.479, *t*(8)=-3.475, *p*=.004; Beta: *M*=-.299, *SD*=.325, *t*(8)=-2.755, *p*=.013) and adults (Mu: *M*=-1.281, *SD*=.502, *t*(9)=-8.064, *p*<.001; Beta: *M*=-.573, *SD*=.341, *t*(9)=-5.315, *p*<.001). The 8-month-olds showed significant suppression of Mu-power (*M*=-.273, *SD*=.382, *t*(9)=-2.257, *p*=.025), but not Beta-power (*M*=-.001, *SD*=.433, *t*(9)=-.013, *p*=.495). Consequently, the 8-month-olds were excluded from further analysis of conditional differences in Beta-power.

Motor processing

Error vs. correct

Results of the mixed ANOVA for Mu-power (Table 2B) showed no significant main effect of Condition

(F(2,29)=.001, p=.976) and no significant interaction between Condition and Age Group (F(2,29)=1.755, p=.191). The main effect of Age Group was marginally significant (F(2,29)=2.701, η_p^2=.157, p=.084). T-tests showed no differences between 8- and 14-month-olds (t(20)=-.944, p=.357), or between 8-month-olds and adults (t(20)=1.486, p= .158). There was however a marginally significant difference between 14-month-olds and adults (t(18)=2.011, p=.060), indicating more overall suppression of Mu-power for adults (M=-.416, SD=.487) compared to 14-month-olds (14m: M=-.095, SD=.137, 8m: M=-.180, SD=.254).

Outcomes of the mixed ANOVA testing for differences in Beta-power showed a main effect of Age Group (F(1,18)=8.068, η_p^2=.310, p=.011) and an interaction of Condition and Age Group (F(1,18)=5.840, η_p^2=.245, p=.027) (Figure 3)[1]. There was no main effect of Condition (F(1, 18)=1.264, p=.276). Paired-samples t-tests showed significantly lower Beta-power for the erroneous compared to the correct condition in adults (Error: M=-.393, SD=.227, Correct: M=-.232, SD=.208, t(9)=4.418, p=.002) and no significant differences for 14-month-olds (Error: M=-.034, SD=.208; Correct, M=-.093, SD=.247 t(9)=-.705, p =.498).

Condition vs. baseline

We further tested for general power suppression during observation (Table 2C) using one-tailed one-sample t-tests per age group. If no significant differences between conditions had been found in the mixed ANOVA, power values were averaged over conditions. All groups showed significant suppression of Mu-power (Figure 4)[1] during action observation (8m: M=-.180, SD=.254, t(11)=-2.451, p=.016; 14m: M=-.095, SD=.137, t(9)=-2.190, p=.028; adults: M=-.416, SD=.487, t(9)=-2.706, p=.012).

For Beta-power, results showed significant suppression for adults (Error: M=-.393, SD=.227, t(9)=-5.473, p<.001, Correct: M=-.232, SD=.208, t(9)=-3.528, p<.001) but not for 14-month-olds (Error: M=-.034, SD=.197, t(9)=-.550, p=.298, Correct: M=-.093, SD=.247, t(9)=-1.190, p=.133).

[1] For illustration of the effect over frontal, parietal and occipital scalp sites see Supplementary Figures.

Visual processing

The mixed ANOVA testing for effects in posterior Alpha revealed a significant main effect of Condition ($F(1,29)=5.447$, $\eta_p^2=.158$, $p=.027$) and Age Group ($F(2,29)=7.747$, $\eta_p^2=.348$, $p=.002$). The interaction between Condition and Age Group was not significant ($F(2,29)=.618$, $p=.546$). Separate t-tests showed significantly lower Alpha for the correct ($M=-.297$, $SD=.422$) compared to the error condition ($M=-.228$, $SD=.456$) across age groups ($t(31)=-2.3$, $p=.028$) and significantly lower Alpha for infants (8m: $M=-.427$, $SD=.274$, $t(20)=4.019$, $p=.001$; 14m: $M=-.439$, $SD=.450$, $t(18)=-3.03$, $p=.007$) compared to adults ($M=.108$, $SD=.350$), but no differences between the two infant groups ($t(20)=.078$, $p=.939$).

Time-resolved and topographic analysis for adults

The TFR (Figure 5a, top) illustrates the power differences between conditions over central sites. Lower power for the error condition was observed in the Beta-band emerging while the observed error unfolds (0-4000ms), but not during the ambiguous movement period (<0ms). Combined, this suggests a time-locked increase in motor activation during error detection. No such reduction was apparent in the Mu-band. In contrast, the TFR illustrating the comparison of conditions over occipital sites (Figure 5a, bottom) shows a conditional difference in the Alpha-range. More precisely, posterior Alpha-power was higher for erroneous than correct actions, potentially suggesting more visual attention allocated to correct actions.

The differential visual processing was also represented in the topographic distribution of the Alpha-power (Figure 5b) spreading over occipital sites. In comparison, the Beta-effect appeared clearly confined to central sites.

Analysis of individual Mu and Beta-frequency ranges

As suggested by Cuevas and colleagues (2014), an alternative approach for infant EEG frequency analysis is determining the individual frequency ranges rather than using a group average. Since this

method can potentially increase the sensitivity of our analysis, we conducted the same analysis as described above using individual frequency ranges for each participant. The exact analysis procedures and all results are described in detail in the supplementary material. Mostly, the results confirmed previous findings, but two relevant differences are reported below.

Action execution vs. baseline

In contrast to the average approach, also 8-month-olds showed Beta-power suppression when using individual frequency ranges (M=-0.259, SD=.285, t(5)=-2.23, p=.038, one-tailed).

Condition vs. baseline

In contrast to the average approach, 14-month-olds, but not 8-month-olds, did show marginal significant suppression of Beta-power for both conditions compared to baseline when using individual frequency ranges (Error: M=-.118, SD=.193, t(8)=-1.838, p=.052; Correct: M=-.142, SD=.250, t(8)=-1.704, p=.064; both one-tailed).

Discussion

It is an observer's challenge to interpret whether a perceived action represents an error. Experience with actions might help us to determine whether an action was accidental or performed on purpose. In our study, stimulus videos depicted authentic errors. The actors had been instructed to grasp small objects without visual access to the objects' position resulting in realistic grasping errors.

In the current study, we investigated to what extent the motor system of infants and adults is involved in monitoring others' errors. The findings suggest that the motor system of adults but not yet infants is modulated by action correctness. In accordance with our hypothesis, oscillatory activity indicated enhanced motor activation for the observation of erroneous as compared to correct grasping actions in adults. Consistent with results of Koelewijn and colleagues (2008), this modulation was indicated by attenuation in Beta-power over central sites. Contrary to our expectations, neither infant group displayed this error sensitivity in their action mirroring. Fourteen-month-olds, as opposed to 8-month-olds, showed indications for suppression of power during action observation not only in the Mu- but also in the Beta-band, indexing activation of their motor system. Nevertheless, we found no indications that 14-month-olds distinguished the correctness of the observed actions with their motor system.

Suppression of Mu-power, one neural marker of mirroring (e.g. Marshall & Meltzoff, 2011), was found during action observation for all age groups, but it was not modulated by action correctness. This suggests a distinct role of Mu- and Beta-oscillatory activity for processing others' errors. In particular, the findings of this study show different patterns of Mu- and Beta-band activation in action monitoring across and within age groups. Unlike Mu-power, Alpha-power over occipital sites was significantly more suppressed during the observation of correct actions across age. Thus, the data further suggest that infants, like adults, differentiate correct from erroneous actions in their visual system. In the following, we discuss the role of different brain oscillations for the development of error monitoring in particular and mirroring in general.

Mirroring: Mu-band activity

In line with previous research (Meltzoff & Marshall, 2011; Vanderwert, Fox & Ferrari, 2012), our findings demonstrate suppression in the Mu-frequency band during action execution and observation across age groups. However, our findings did not confirm a modulation of Mu-power by the actions' correctness. Pineda (2005) proposes the Mu-rhythm to be involved in "translating 'hearing' and 'seeing' into doing"(p.57). Research on the topographic distribution of Mu-band activity supports this interpretation (Ritter, Moosmann & Villringer, 2009): Mu-activity was associated with origins more posterior than Beta-activity, bridging motor and sensory regions. In the same vein, Mu-activity has been linked to research on vision-to-action in the context of observational and imitation learning (Bernier et al., 2007). Infant EEG work has shown that Mu-band activity is also involved in action predictions (Southgate et al., 2010) and their violations (Stapel et al., 2010). Yet, our findings did not show any indications for involvement of Mu-oscillations in error processing. Rather, we found suppression for both erroneous and correct actions. In line with Koelewijn and colleagues (2008), the detection of errors might be specific to the functionality of Beta-oscillations. While Mu- and Beta-activity share functional involvement in action processing, they might diverge in their involvement in error detection. Future research is needed to disentangle commonalities and differences of Mu- and Beta-band activity for processing others' actions (see also Meyer et al., 2011).

Mirroring and error monitoring: Beta-band activity

In contrast to the Mu-suppression present across age groups, our data suggest a gradual emergence of Beta-suppression in processing own and others' actions. Adults showed Beta-suppression during execution and error-sensitive suppression during observation. This finding extends the current literature by providing evidence for error monitoring in the motor system not only for rule-based but also for everyday action errors (such as accidentally dropping something). In 14-month-olds, we found Beta-suppression during execution and indications for suppression during action observation, indicating general mirroring insensitive to action correctness. Finally, suppression of Beta-activity was

evident only during action execution in the 8-month-olds and only using a more sensitive individual frequency approach. This raises the question, what the function of Beta-suppression is and what underlies its age-related differences.

In adults, we found Beta-power attenuation during action execution and observation to be locally confined over sensori-motor sites. Findings from combined EEG and fMRI measurements support the association of Beta-power with motor cortical activity originating from the primary motor cortex and pre-motor areas (Ritter, Moosmann & Villringer, 2009). Furthermore, in adults Beta-power was more strongly suppressed during the observation of erroneous actions which in functional terms could be interpreted as the detection of a violation from an expected action. On the basis of own action experience, feed-forward processing could activate potential upcoming events during the observation of others' actions. In case the observed event does not match the prediction, a violation would then be detected and reflected in enhanced motor processing. In congruence with this, recent MEG findings suggest that Beta-band activity reflects top-down processing of predictions and their violations (Arnal, Wyart, & Giraud, 2011). Arnal and colleagues (2011) further suggest that, via backward propagation, Beta-band activity is involved in updating violated predictions. Similarly, Engel and Fries (2010) put forward the hypothesis that Beta-band activity signals the maintenance of a current state. In that function, Beta-band activity is sensitive for deviations between the current and expected state. The current results and findings by Arnal and colleagues (2011) fit in the framework of this maintenance hypothesis in which Beta-band activity is sensitive to violations of current and expected states.

In contrast to Beta-effects in adults, current observations in the infants did not show error sensitivity. This result was unexpected for the 14-month-oldsas they had the fine-motor skill of grasping small objects and showed general mirroring as indexed by Beta-suppression when assessing individual frequency ranges. One possible explanation for this finding is that these infants still lack sufficient grasping experience to discern the two actions the way adults do. Although 14-month-olds are able to successfully grasp small objects, their experience is limited to a few months and differs by

years of extensive training from adults'. At this intermediate level of motor skills stable feed-forward predictions in the motor system and respective prediction errors might not be fully established yet. A lack of fine-motor skills might explain that 8-month-olds did not display significant Beta-suppression during action observation at all.

Another explanation of the data might be reflected in methodological challenges associated with capturing sensori-motor processes in action execution and observation in higher oscillatory frequencies in infants. The observed Beta-suppression in the 14-month-olds was significant but small using individual frequency ranges, whereas 8-month-old infants did not show any significant Beta-suppression during action observation. An MEG study confirmed very low suppression effects for 4-year-olds in Beta-band activity during action execution (Gaetz et al., 2010). Since higher frequencies generally have a lower signal-to-noise ratio the chances of picking up conditional differences are diminished, especially in studies with limited data quality for instance with developmental populations.

Still, indications of Beta-band reactivity to action execution in both infant groups and action observation in 14-month-olds add to the scarce findings on Beta involvement in action processing during infancy (cf. van Elk et al., 2008). The emergence of Beta-band reactivity to action processing is matter of current research (Gaetz et al., 2010; Cheyne et al., 2014) but has mainly focused on pre-school and school-aged children. Developmental changes in the levels of inhibitory neurotransmitters were proposed as one factor for age-related changes in Beta-band reactivity (Gaetz et al., 2010). Moreover, maturational changes in connectivity between motor cortex and subcortical areas may influence Beta-oscillatory activity (Gaetz et al., 2010; Cheyne et al., 2014). Nezu and colleagues (1997), for instance, observed a strong decrease in conduction times of the corticospinal motor pathway especially between the ages of one and two years. Analogously, the current results which indicate expansion of Beta-reactivity from action production to action observation is observed between infants in their first and their second year of life. Yet, to what extent age-related changes in

connectivity and levels of inhibitory neurotransmitters might underlie the current findings remains speculative.

Summarizing, the current findings offer a starting point for future research which is needed to track the developmental trajectory and investigate changes in functionality of Beta-oscillatory activity from infancy to adulthood.

Motor versus Visual Processing

Whereas we observed changes in action monitoring within the motor system over age, all groups showed decreased visual Alpha-power over occipital sites for correct compared to erroneous actions. The functional distinction of Mu- and posterior Alpha-activity is in accordance with previous research (Frenkel-Toledo et al., 2013; Pineda, 2005). A reduction in posterior Alpha has been associated with enhanced attention in the visual system (Thut et al., 2006); therefore the measured reduction in posterior Alpha suggests that more visual attention was devoted to the correct action. Although it remains unclear what exactly leads to this attention difference, it is interesting that in adults, motor activity (as indexed by Beta-suppression) is enhanced for erroneous actions while visual activity is enhanced for correct actions. This finding suggests distinct cross-modal processing in adults allowing parallel evaluation of observed actions with respect to visual and motor features.

Conclusion

Taken together, the degree to which the motor system is involved in monitoring others' actions in general and their errors in particular changes across development. Mu- and Beta-band oscillations over motor regions show a distinct pattern of activation from infancy to adulthood suggesting functionally distinct roles in action monitoring. Power in the Mu-rhythm was involved in mirroring but not modulated by the correctness of actions. However, suppression in Beta-power was modulated by action correctness and emerged with age. Young infants only showed suppression in action execution, whereas indications of mirroring were apparent for older infants and adults. In

addition, adults showed error-sensitivity in motor-related Beta-oscillations, likely reflecting the detection of a violation of expectation. Thus, infants and adults involved their motor system to a different extent during the observation of others' errors. In contrast, infants and adults processed the visual features of others' actions in a similar manner.

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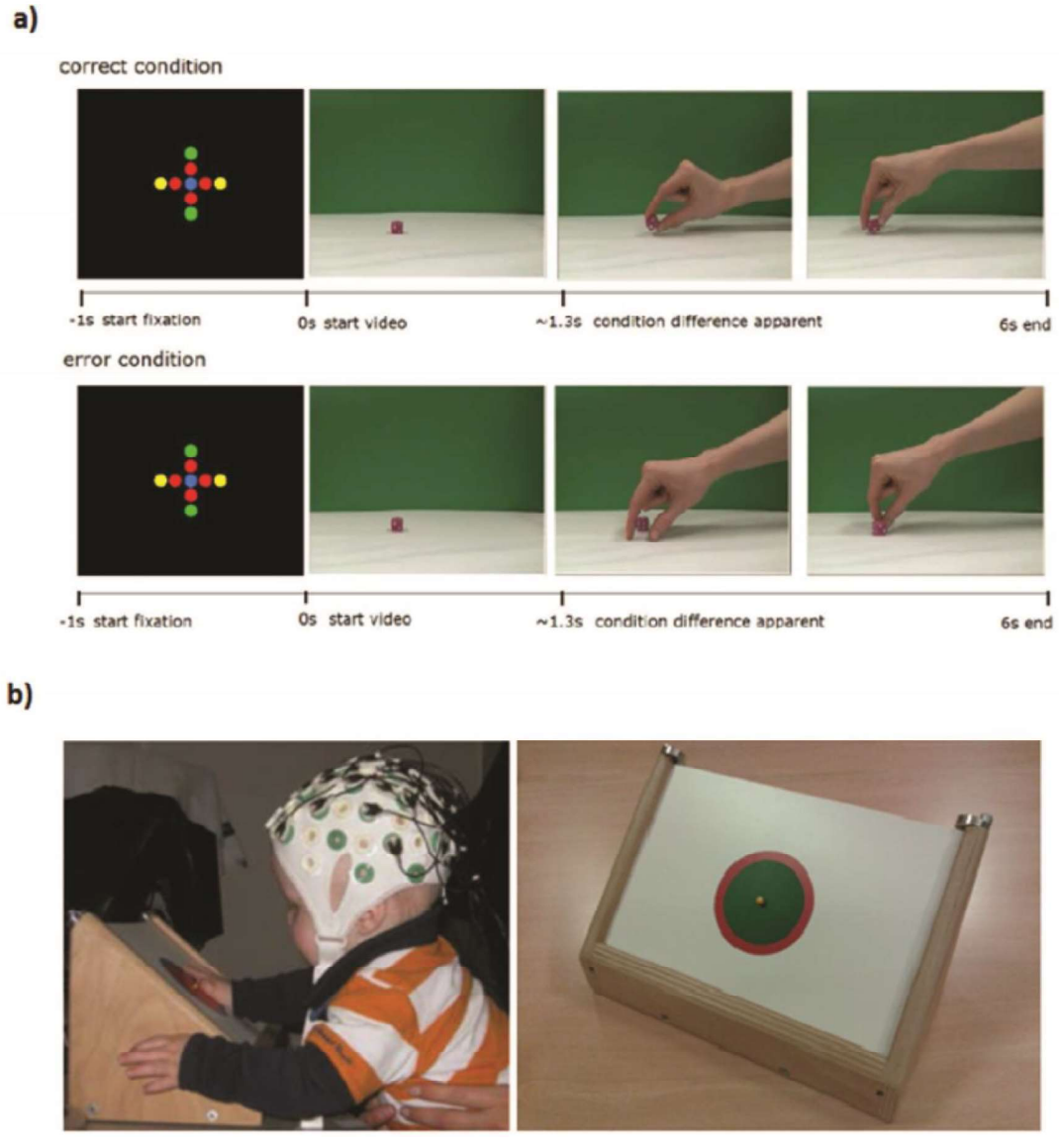


Figure 1.
Overview of the stimuli, materials and example of action execution. a) Illustration of visual stimuli, starting with a still image of a fixation cross, followed by video clip of a correct (top) or erroneous (bottom) pincer grasp action. Only periods in which condition differences were apparent were included in the statistical analysis between conditions. b) Grasping device with the larger of two beads (right picture) and example of action execution phase during EEG measurement.

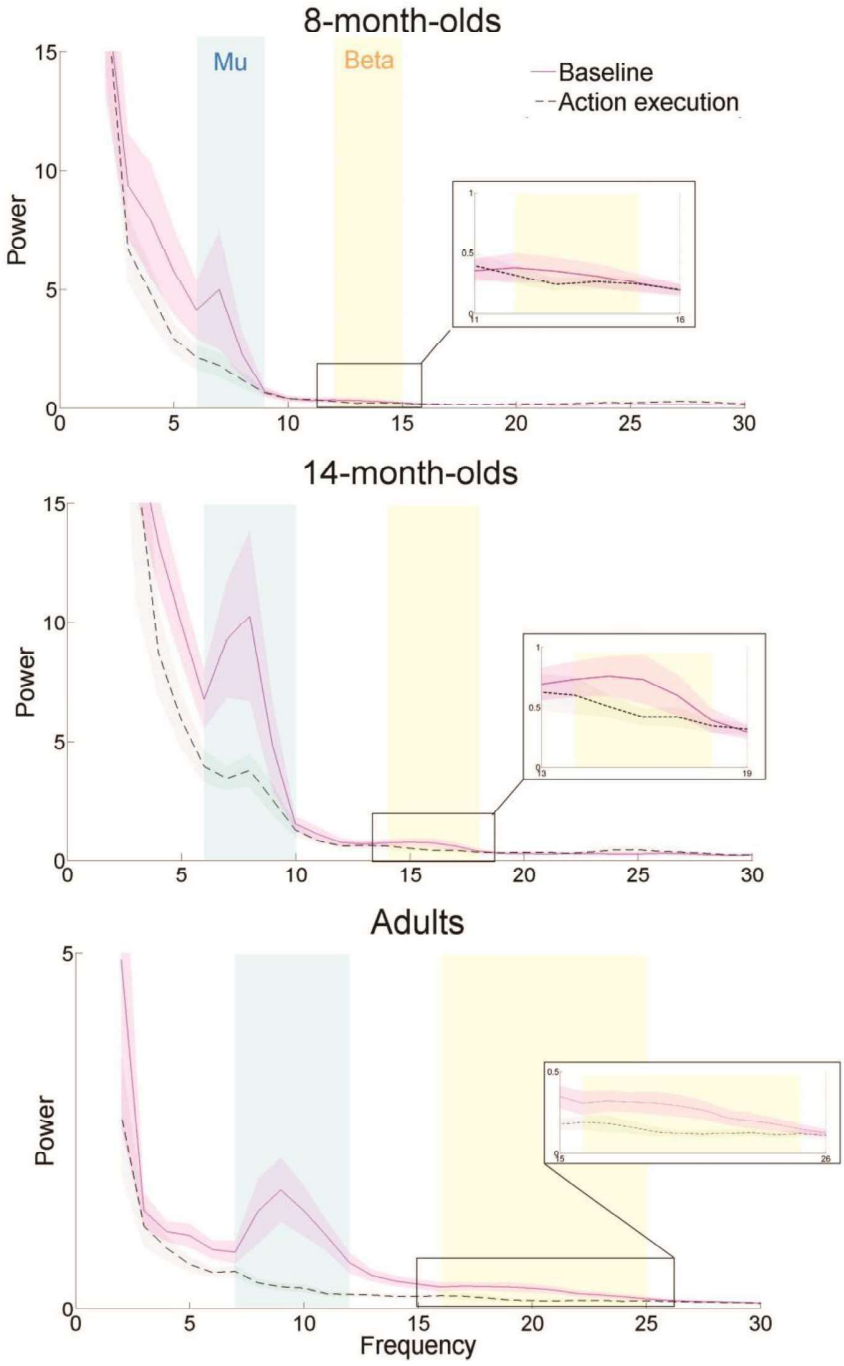


Figure 2.

Power values as a function of frequency (Hz) depicted for baseline and execution of grasping actions (baseline, pink solid line; execution, black striped line), separately for age groups. Pink and black shaded areas represent the standard error of the baseline and execution power values, respectively. Blue shaded areas illustrate the selected Mu-frequency range and yellow shaded areas illustrate the Beta-frequency range per age group.

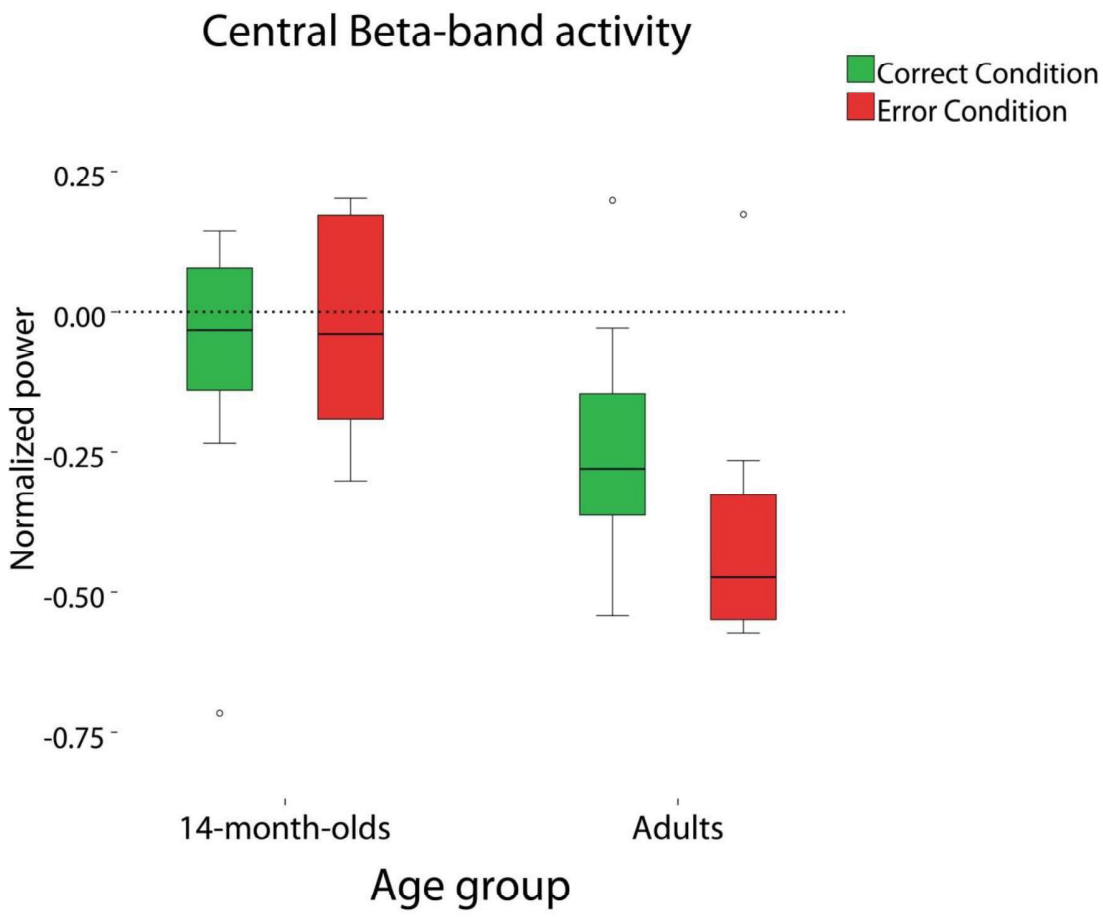


Figure 3.
Boxplots of normalized Beta-band power are depicted separately for Condition (correct/error) and Age Group (14-month-olds, adults). Whereas the 14-month-olds do not show differences between conditions, the adults show enhanced suppression for the error condition.

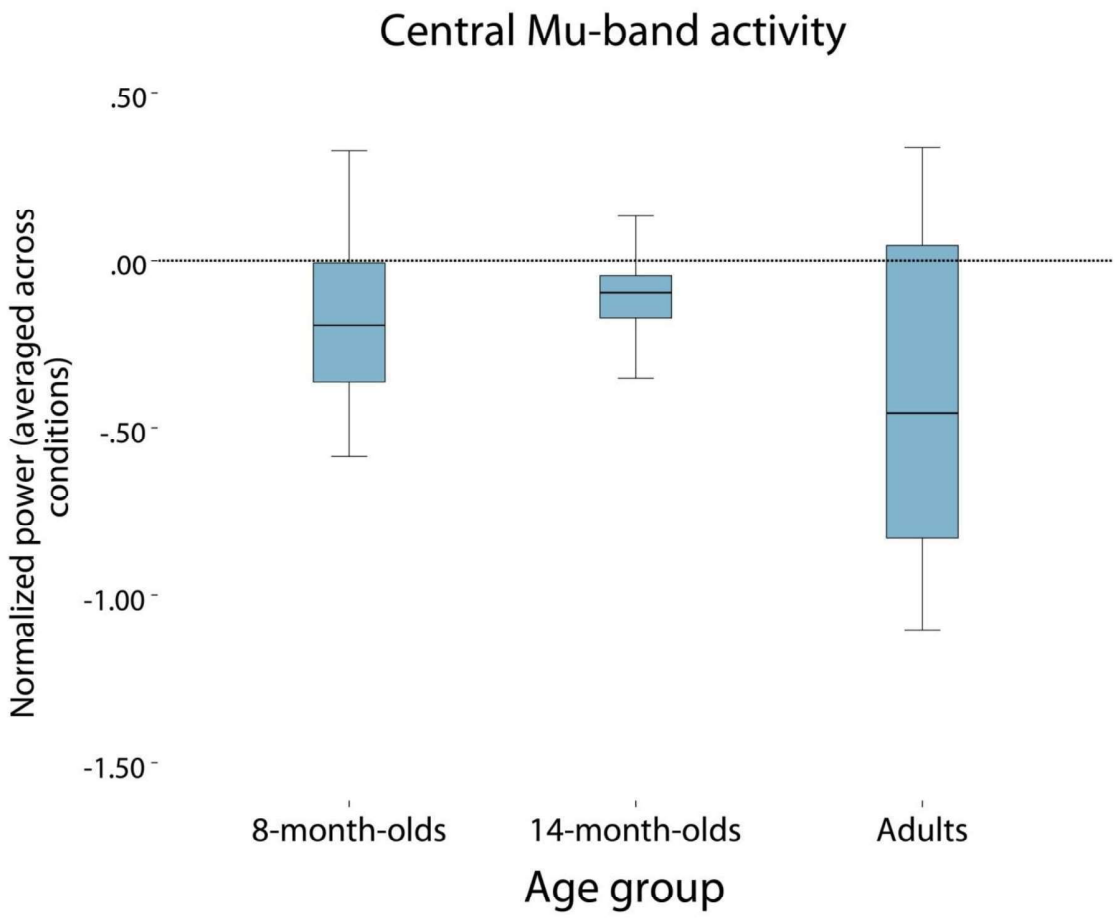


Figure 4.
Boxplots of normalized Alpha-band power averaged across conditions are depicted separately per Age Group (8-month-olds, 14-month-olds, adults).All age groups show significant suppression of Mu-power during action observation.

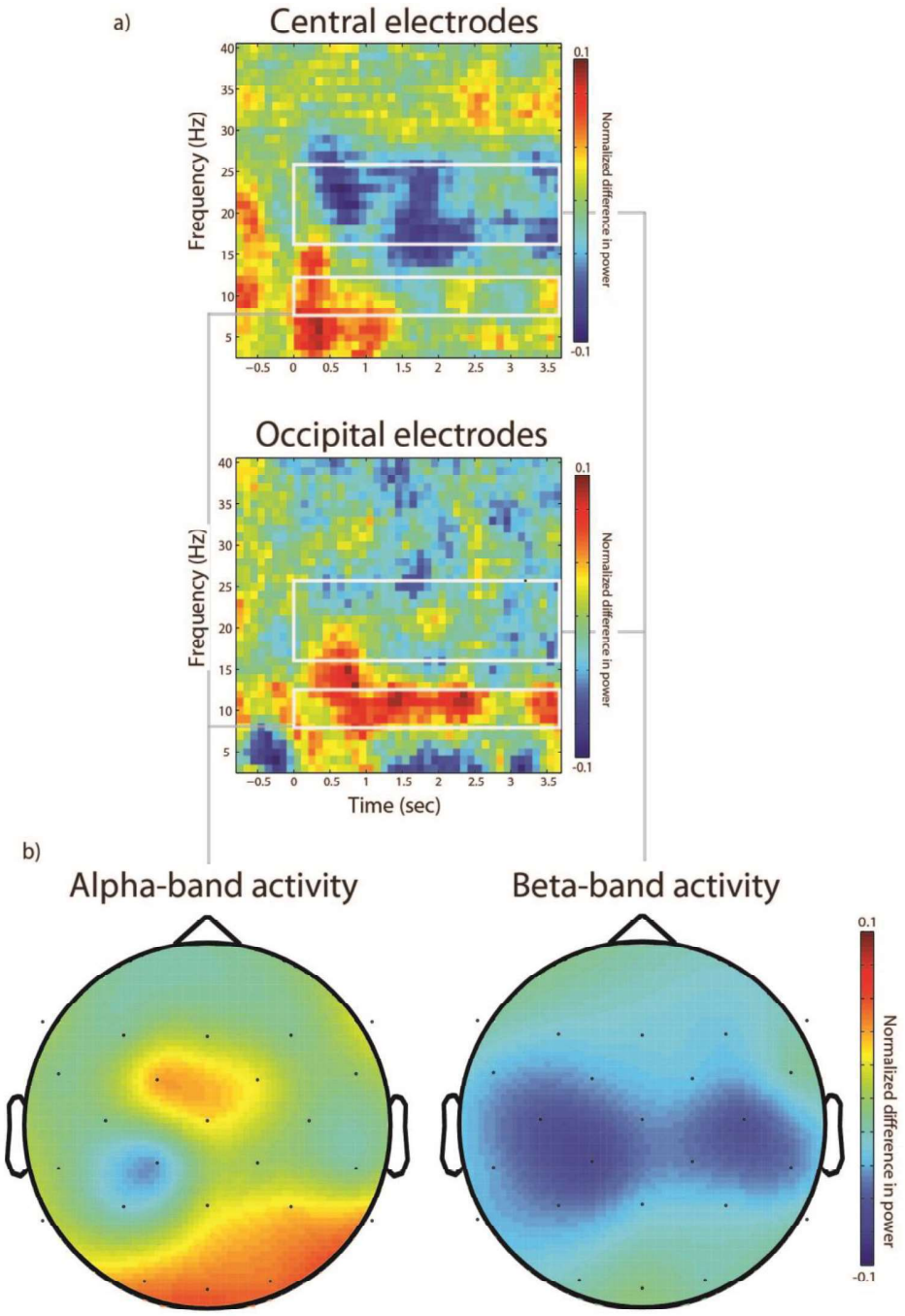


Figure 5.

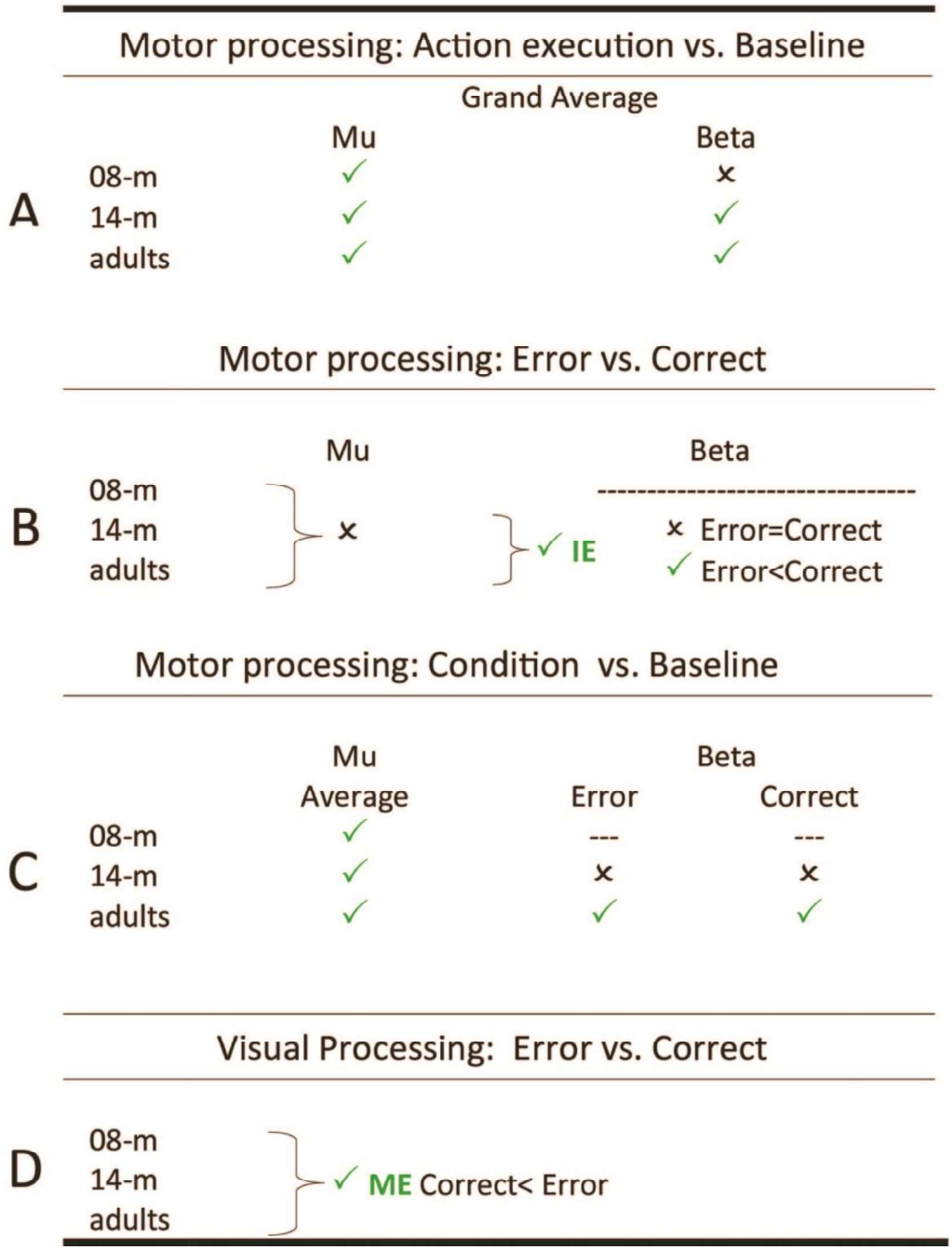
Time-frequency representations and topographic distribution of power differences during action observation for the adult group. a) Depicted are time-resolved normalized difference values in power at central (top) and occipital (bottom) electrode sites. Power differences represent a direct comparison of power during action observation between the erroneous and correct grasping action ([error-correct]/[error+correct]). At time 0, differences between correct and erroneous types of grasping emerge and unfold during the period of 0s to 4s. Before time 0, video stimuli depict a hand reaching towards a small object in the scene. White boxes indicate the period of interest in which the stimuli differ in correctness of the action (0s to 4s) and the frequency ranges of interest (Alpha: 7-12Hz; Beta: 16-25Hz). Topography of normalized Alpha- (left) and Beta-band power differences (right) deduced from these time-frequency windows are illustrated in b). Warm colors represent higher power for the error condition compared to the correct condition and cooler colors represent lower power for the error condition.

Table 1.

Characteristics of the final sample. *Please note that for the analysis of the action execution condition, two 8-month-old infants and one 14-month-old infant had to be excluded due to no artifact-free data.

Sample characteristics				Mean number of trials (std)			
Age group	N	Mean age (std)	Gender (f:m)	Baseline	Correct condition	Error condition	Action execution
08-m	12	8.13(0.21)	4:8	20.00 (8.05)	21.33(16.90)	21.83(15.44)	17.7(9.58)*
14-m	10	14.04(0.24)	5:5	14.00 (6.38)	17.00(6.98)	21.20(9.94)	24.7(14.66)*
adults	10	27(4.1)	5:5	31.60(20.34)	87.50(15.98)	91.70(14.26)	9.9(0.57)

Table 2.



An overview of results from the EEG data analysis. Significant results are marked in green. Part A shows the results from the t-tests comparing action execution to baseline. In part B the results of the mixed ANOVAs testing for group and condition differences are displayed. The results of the t-tests assessing general suppression during action observation are illustrated in part C. Part D gives an overview of the results from the ANOVA testing for group and conditional differences in visual processing. IE: Interaction effects, ME: Main effects.